

ICES C.M.2004/K:26

A closed life-cycle model for Northeast Arctic cod

Bjarte Bogstad, Daniel Howell and Morten Nygaard Åsnes, Institute of Marine Research, Bergen, Norway

Abstract

For Northeast Arctic cod (*Gadus morhua*), there is much knowledge available concerning the main population dynamics processes (growth, maturation, fecundity, recruitment, natural mortality, fishing mortality). This knowledge is incorporated into a biologically detailed age-length structured population model. The model contains four population groups: EggsandLarvae, 0-group, immatures (age 1-10) and matures (age 4-12+). Recruitment to EggsandLarvae is modelled as a function of the number of mature fish and their population characteristics (length and weight), giving a fully closed life cycle. The model is implemented using the Gadget framework for population models, and the details of the implementation are described here. Results of fitting the population model to observations are presented. The utility of such a model in the assessment of current stock status and the exploration of harvest control rules is discussed.

1. Introduction

At IMR, Bergen, Norway, work on the Fleksibest model for Northeast Arctic cod has been going on for some years (Frøysa et al., 2002; ICES, 2004b). This is a biologically-detailed age-and-length structured model, where mortality, growth and maturation are modelled as functions of length and weight, and possibly age. The cod stock is divided into mature and immature components. In order to incorporate more of the biological knowledge available for this stock, the model is being extended to include a closed life-cycle. This WD outlines how this can be done using the Gadget model framework (Anon., 2003a; <http://www.hafro.is/gadget>). Such a model will be able to incorporate research presented to SGPRISM (ICES, 2002) and SGGROMAT (ICES, 2003a; 2004a) in recent years, and provide a framework to incorporate future developments into an existing population model. In this paper we first describe the division of cod into population groups, and how the movement between population groups takes place. Then we describe the model structure (time step, length groups, age groups, which kind of mortality applies to each population group, spawning time etc.) This is followed by a review of the equations describing the population dynamics processes maturation, fecundity, mortality and growth. Finally we present results of fitting the model to the available data.

This paper shows how the Gadget framework can be used to incorporate such models, using Northeast Arctic cod as an example. A discussion of how and why more biological knowledge should be included in stock assessment is given by Ulltang (1996).

2. Model structure

Figure 1 illustrates the division into population groups. All individuals within a single population group share the same equations governing their biological processes.

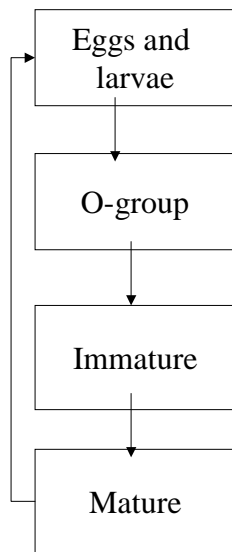


Figure 1. Movement between population groups in closed life-cycle model for Northeast Arctic cod

Time step: quarter (could be changed to month later)

Time period: 1985-2004, last time step in model is quarter 1 in 2004.

3. Population group descriptions

Movement of fish between population groups is either by the *Move* or the *Maturation* function. *Move* means that all individuals move to the new stock at a specific time, while a *Maturation* function allows the transition between population groups to be based on age and/or length.

3.1 Eggs and larvae

Spawned at end of quarter 1 (31 March). Hatched in quarter 2.

Age: 0

Length group width: 0.5 cm

Length range: 1-15 cm

Mortality: Very high, year-dependent residual natural mortality in quarter 2, otherwise no mortality.

Moves: to 0-group at 30 June (end of quarter 2)

Length distribution (mean length, standard deviation) given.

Growth: None. Mean length and standard deviation are model parameters (these are in reality the corresponding parameters for 0-group).

Except for the mortality, this stock is a dummy stock to which nothing happens. It is introduced to allow for a delay between spawning and time of recruitment as 0-group fish. Having *Eggs and larvae* as a separate stock also allows for the effects of larval drift in future multi-area models.

3.2 0-group

Age: 0

Length group width: 0.5cm

Length range: 1-20cm

Mortality: Cannibalism (quarter 4 only), residual natural mortality (possibly year-dependent)

Moves: to immatures at end of quarter 4 (December 31)

Growth: See section 4.4

3.3 Immature

Age range: 1-10

Length group width: 1 cm

Length range: 5-105 cm

Mortality: Fishing, Cannibalism, residual

Predator: Cannibal on immatures and 0-group

Growth: See section 4.4

Maturation function: See section 4.1. Applied at end of quarter 4 (31 December). Immature fish mature into mature fish

3.4 Mature

Age range: 4-12+

Length group width: 1 cm

Length range: 45-135cm

Mortality: Fishing, Cannibalism, spawning, residual

Predator: Cannibal on immatures and 0-group

Growth: See section 4.4

Spawning time: 31 March (end of quarter 1)

Spawning mortality: None

Spawning weight loss: Not modelled in this version since we do not directly model growth in weight, but read weight at length for each population group in each time step (Section 4.4)

4. Equation describing population dynamics processes

Symbols used:

t: time

y: year, $= [t/4] + 1$, where $[]$ denotes the integer part of the argument

q: quarter, $= \text{mod}(t, 4) + 1$

i, j: length groups

L_0 : Minimum length of length group 1 (smallest length group)

ΔL : width of length groups

L_{\max} : number of length groups

l_i : mean length of fish in length group i , $l_i = L_0 + (i - \frac{1}{2})\Delta L$, $i=1, L_{\max}$

a: age

u, v: population group

U: number of population groups

$\underline{N}_u(t)$: vector of length L_{\max} , number of fish in population group u at time t
 $N(u,i,t)$: number of fish in i -th length group of population group u at time t
 $W(u,i,t)$: mean weight of fish in i -th length group of population group u at time t
 f : fleet index
 p : survey index
 T : temperature ($^{\circ}\text{C}$)

For simplicity, the model description given here assumes that L_0 , ΔL and L_{\max} are the same for all population groups, although this is not the case for the population groups described in Section 3, and will usually not been the case. The Gadget software permits differing population groups to have different length groups, providing that the finer length groups are exact subdivisions of the larger ones.

We consider a model where survival, growth, maturation and recruitment only depend on the length and weight of the fish, but not on the age. Thus the index for age can be omitted in the description, and the state variables can be described by the vectors $\underline{N}_u(t)$. The model is structured by age and length groups, but the age of the fish is only taken into account when comparing the model to observations (Section 5). It is possible to extend this within the Gadget framework to model age-dependant processes if this is deemed necessary.

During a time step, mortality is applied before growth. Following Frøysa et al. (2002), the connection between stock abundance before and after mortality and growth takes place can be written as

$$\underline{N}_u^{(1)}(t) = S_u(t) \underline{N}_u(t) \quad (1)$$

and

$$\underline{N}_u^{(2)}(t) = G_u(t) \underline{N}_u^{(1)}(t) \quad (2)$$

where $S_u(t)$ and $G_u(t)$ are $L_{\max} \times L_{\max}$ matrices which describe survival and growth, respectively.

During a time step where only survival and growth takes place, we have:

$$\underline{N}_u(t+1) = \underline{N}_u^{(2)}(t) \quad (3)$$

For a more general matrix description of such models, including maturation and recruitment, see Frøysa et al. (2002).

4.1 Maturation

We use equation (4) to describe the probability of an immature fish becoming mature, assuming that this remains constant throughout the model period. Maturation is assumed to occur at the end of the year (quarter 4).

$$P_{mat}(a,i,t) = \frac{1}{1 + e^{-4\alpha (l_i - l_{50}) - 4\theta (a - a_{50}) - 4\lambda \left(\frac{W_{a,i,t}}{W_{ref}(l_i)} - K_{50} \right)}} \quad (4)$$

The first term in the exponential function gives the length dependence of the maturation. If we assume the two other terms to be zero, l_{50} denotes the length at which 50% of the fish will become mature, while α denotes the rate of change of maturation when $l = l_{50}$. Similarly, a_{50} denotes the age at which 50% of the fish will become mature, while θ denotes the rate of change of maturation when $a = a_{50}$. Setting θ to zero removes the influence of age on maturation. The last term is more complicated. It describes how the maturation depends on the condition of the fish. The probability of maturing will be increased for a fish heavier than the average suggested by the length-weight relationship, and reduced for one with a weight below the length-weight relationship. K_{50} , the ratio between actual weight at length and reference weight at length for which this last term is equal to zero, is normally set to 1.0. λ describes how strongly maturation depends on the length-weight relationship. If the weight is equal to the reference weight for that length, this last term will be equal to zero.

The proportion maturing described by equation (4) is the same as the reaction norm (see e.g. Heino et al., 2002), defined as the maturation probability of immature fish given that they have reached a certain age and size. We assume that maturation does not depend on age, i.e. $\theta=0$, a_{50} is then irrelevant.

The reference weight parameters are obtained externally to the model. The following length (cm)- weight (kg) relationship has been obtained by pooling all available data for 50-140 cm fish in the period 1946-2001 (ICES, 2003a).

$$W_{ref}(l) = 0.000008 l^{3.01} \quad (5)$$

If $\lambda = 1.2$, and $K_{50} = 1$, a change in condition factor of 20% from the reference value will give approximately an 8 cm change in length at 50% maturation, which fits with the data for proportion mature in Icelandic cod (ICES, 2003a). Very low values for the proportion mature at length have also been observed for Northeast Arctic cod in years with low weight-at-length (Marshall et al., 1998).

4.2 Fecundity

The main reason for modelling fecundity is that the correlation between total egg production, TEP, and recruitment at age 3 for Northeast Arctic cod is stronger than the correlation between spawning stock biomass and recruitment (Marshall et al. 2003). In addition, Marshall et al. (2000) found that for NEA cod, the correlation between total lipid energy in year y and recruitment to age 3 for spawning year $y+1$ is stronger than the corresponding relationship between spawning stock biomass and recruitment.

Bogstad (2003) suggested the following formulation of TEP for use in Gadget:

$$TEP(t) = \sum_{a,i} N(v, a, i, t) Fec_{v,a,i} = \chi \sum_{a,i} N(v, a, i, t) l_i^\alpha W(v, a, i, t)^\beta \quad (6)$$

where the subscript v denotes mature female fish. TEP is thus dependent on numbers, length and weight of mature females.

ICES (2003b) give the following equation for fecundity (million eggs) for fish in length group i of Northeast Arctic cod:

$$Fec_{i,t} = 4.179 \cdot 10^{-7} l_i^{3.52} Kn_{i,t}^{2.16} \quad (7)$$

where $Kn_{i,t}$ is the relative condition factor, given by

$$Kn_{i,t} = \frac{W(i,t)}{W_{ref}(l_i)} \quad (8)$$

and the reference weight $W_{ref}(l_i)$ is given by

$$W_{ref}(l_i) = cl_i^b \quad (9)$$

For pre-spawning females, the following length (cm)-weight (kg) relationship has been established (ICES, 2003a):

$$W_{ref}(l) = 0.0000049 l^{3.18} \quad (10)$$

The difference between the length-weight relationship for pre-spawning females (10) and the overall length-weight relationship (5) may be due to biological difference (the build-up of gonads may affect the length-weight relationship). However, (10) is based on a much smaller data set and a much shorter time series than (5), which also may be the reason for the difference. More work is required to identify the major reason for this difference.

Inserting (8) and (10) into (7), this gives

$$Fec_{i,t} = 4.179 \cdot 10^{-7} l_i^{3.52} \frac{W(i,t)^{2.16}}{0.0000049^{2.16} l_i^{2.16 \cdot 3.18}} \quad (11)$$

or

$$Fec_{i,t} = 123097 l_i^{-3.3488} W(i,t)^{2.16} \quad (12)$$

which can be used in equation (6), assuming the fecundity of female fish to be independent of age, i.e. $Fec_{a,i,v,t} = Fec_{i,t}$. For a 100cm, 10 kg cod this gives a fecundity of 3.57 million eggs. Assuming a 1:1 sex ratio, equation (12) can be written

$$Fec_{i,t} = 61549 l_i^{-3.3488} W(i,t)^{2.16} \quad (13)$$

when the mature stock is not divided by sex.

4.3 Mortality

The number caught by fishing and eaten by cannibalism during each time step is calculated as described in sections 4.3.1 and 4.3.2, while spawning mortality and residual natural mortality

are modelled as rates. The number of fish after mortality has taken place during a time step, $N^l(u, i, t)$, is then given by:

$$N^l(u, i, t) = (N(u, i, t) - C(u, i, t) - D(u, i, t))e^{-M1(u, i, t) - M3(u, i, t)} \quad (14)$$

where C is the number caught by fishing, D is the number eaten due to cannibalism, $M1$ is residual natural mortality and $M3$ is spawning mortality.

4.3.1 Fishing mortality

The catch in biomass by each fleet f of fish length group i and population group u during a time step is assumed to be proportional to the biomass of available prey in that group, and the fishing effort. The biomass of available prey of length group i and population group u for fleet f at time t is given by

$$B_f(u, i, t) = N(u, i, t)W(u, i, t)\Xi_{f,u}(l_i) \quad (15)$$

where $\Xi_{f,u}(l)$ ($0 \leq \Xi \leq 1$) is the length-dependent suitability function (selection curve) for population group u and fleet f . A typical suitability function is

$$\Xi_{f,u}(l) = \frac{1}{1 + e^{-4\alpha_{f,u}(l - l_{f,u,50})}} \quad (16)$$

The biomass of fish in length group i of population group u caught by fleet f during time step t , $H(f, u, i, t)$, is then given by

$$H(f, u, i, t) = \zeta_f(t)B_f(u, i, t) = \zeta_f(t)N(u, i, t)W(u, i, t)\Xi_{f,u}(l_i) \quad (17)$$

and the number of fish caught is given by

$$C(f, u, i, t) = \frac{H(f, u, i, t)}{W(u, i, t)} \quad (18)$$

The total modelled catch in numbers by all fleets is then given by:

$$C(u, i, t) = \sum_{f=1}^{N_f} C(f, u, i, t) \quad (19)$$

where N_f is the number of fleets.

For Northeast Arctic cod, we estimate the yearly effort, and assume that the quarterly distribution of the effort within a year is the same as the quarterly distribution of the reported catch in tonnes, i.e.

$$\zeta_f(t) = \zeta_f(y)\theta_{f,q,y} \quad (20)$$

where

$$\theta_{f,q,y} = \frac{H_f(q,y)}{\sum_{q=1}^4 H_f(q,y)} \quad (21)$$

and $H_f(q,y)$ is the reported catch in tonnes by fleet f in quarter q and year y .

4.3.2 Cannibalism mortality

Cannibalism is an important source of mortality for young Northeast Arctic cod. The spatial and temporal variation in cod cannibalism, as well as the predator length- prey length distribution, is described by Bogstad et al. (1994). The consumption by cod is modelled using the same predation model as in MULTSPEC (Bogstad et al. 1997). First the consumption in biomass per predator and time step is calculated. The total consumption per time step is then calculated by multiplying by the number of predators and summing over all predator groups. We consider two prey sources: cod and other food (largely capelin (*Mallotus villosus*)).

Let $D_{\max}(L,T)$ be the maximum consumption rate (kg/time step) by a cod of length L when the temperature is T :

$$D_{\max}(L,T) = \kappa \zeta(T) L^{\delta} \quad (22)$$

The temperature-dependence $\zeta(T)$ is assumed to be the same as in Bogstad et al. (1997), and the exponent δ is set to 2.4 (Bogstad et al. (1997) use $W^{0.8}$, which is equivalent to $L^{2.4}$ if $W = \text{constant} * L^3$). The consumption per predator in population group v and length group j per time step is given by the maximum consumption multiplied by a fraction $\psi(v,j,t)$ (equation 26). This fraction is called the feeding level and denotes the fraction of the maximum consumption that the predator is consuming.

$$D(v,j,t) = D_{\max}(L_j, T(t)) \psi(v,j,t) \quad (23)$$

The seasonal variation in overlap between large (predator) cod and small (prey) cod is strong and should be taken into account even in a model without explicit spatial structure. The mature cod migrates to the Lofoten area to spawn in March-April (Godø 1989), and does not prey on immature cod during this period. We assume that cannibalism by mature cod does not occur during the first quarter. Similarly, 0-group is not subject to major predation by older cod until it has settled to the bottom. This takes place in autumn (Nakken 1994), and thus we assume 0-group to be subject to cannibalism only in the fourth quarter.

We thus assume that the preference of a prey for a predator can be split into a time(overlap)-dependent part and a size-dependent part. Define the biomass of prey group u , length group i suitable for predator group v , length group j as

$$\Phi(v,j,u,i,t) = \Xi(l_i, L_j) \Theta(u,v,t) N(u,i,t) W(u,i,t) \quad (24)$$

Here l denotes prey length and L predator length. We use the model for the size-dependent suitability $\Xi(l,L)$ ($0 \leq \Xi \leq 1$) given by Bogstad (2002):

$$\Xi(l,L) = 0 \quad \text{if } \ln \frac{L}{l} \leq 0 \text{ and}$$

$$\begin{aligned}\Xi(l, L) &= p_0 e^{-\frac{(\ln \frac{L}{l} - p_1)^2}{p_2}} \text{ if } 0 < \ln \frac{L}{l} \leq p_1 \text{ and} \\ \Xi(l, L) &= p_0 e^{-\frac{(\ln \frac{L}{l} - p_1)^2}{p_3}} \text{ if } \ln \frac{L}{l} > p_1\end{aligned}\quad (25)$$

with parameter values $p_0=0$, $p_1=1.12$, $p_2=0.015$, $p_3=0.228$. (As far as I remember from the 2004 AFWG meeting we actually tried to estimate p_1 , p_2 and p_3 !)

The overlap factor $\Theta(u, v, t)$ is set equal to 1, except for the following cases:

$\Theta(\text{immature}, \text{mature}, q)=0$ when $q=1$, and $\Theta(0\text{-group}, \text{immature}, q)=\Theta(0\text{-group}, \text{mature}, q)=0$ when $q=3$.

The feeding level $\psi(v, j, t)$ (equation 26) denotes the fraction of the maximum consumption that the predator is consuming:

$$\psi(v, j, t) = \frac{\sum_{i=1}^{j-1} \sum_{u=1}^U \Phi(v, j, u, i, t)}{H_{1/2} + \sum_{i=1}^{j-1} \sum_{u=1}^U \Phi(v, j, u, i, t) + \text{otherfood}(t)} \quad (26)$$

The ‘half feeding value’ $H_{1/2}$ is the prey density required to allow the predator to consume prey at half the maximum consumption level. We do not model food shortage here, so the ‘half feeding value’ $H_{1/2}$ is set to zero.

Capelin is the main prey item for cod (Bogstad and Mehl 1997). Here we model it as an externally defined other food. Because the variation in capelin abundance is very large (from 0.1 to 7.3 million tonnes in the period 1985-2003, ICES 2003b), we allow for less variation in the abundance of other food than the variation in capelin abundance by setting

$$\text{otherfood}(t) = v \text{Capelin}(t) + \gamma \quad (27)$$

where $\text{Capelin}(t)$ is the capelin biomass at time t . The constant v describes the suitability of capelin for cod, while the constant γ is a measure of the other, non-capelin, food sources available to the cod, and may be estimated within the model. The calculation of capelin biomass at time t is described in Section 5.3. Note that predation by cod does not influence the capelin abundance in this model formulation.

The biomass of cod in population group u and length group i eaten by cod in population group v and length group j is then given by:

$$B(v, j, u, i, t) = \frac{N(v, j, t) D_{\max}(L_j, T(t)) \psi(v, j, t) \Phi(v, j, u, i, t)}{\sum_{i=1}^{j-1} \sum_{u=1}^U \Phi(v, j, u, i, t) + \text{otherfood}(t)} \quad (28)$$

The number of cod in population group u and length group i eaten by cod in population group v and length group j is then given by:

$$D(v, j, u, i, t) = \frac{B(v, j, u, i, t)}{W(u, i, t)} \quad (29)$$

and the total number of cod in population group u and length group i eaten by cod is given by

$$D(u, i, t) = \sum_{v=1}^U \sum_{j=i+1}^{L_{\max}} D(v, j, u, i, t) \quad (30)$$

The formulation given by equations (22-30) is a modification of the cannibalism equation given in Frøysa et al. (2002).

4.3.3 Spawning mortality

The spawning mortality $M3$ is at present set to zero.

4.3.4 Residual natural mortality

For each population group, the residual natural mortality is assumed to be variable only by year, i.e.

$$M1(u, i, t) = M1(u, y) \quad (31)$$

This yearly factor will be estimated for *Eggsandlarvae* and possibly for 0-group. For immature and mature fish, both female and male, we set $M1=0.2 \text{ year}^{-1}$, i.e. no year-dependant effect.

4.4 Growth

4.4.1 Mean growth in length:

The mean length growth can be calculated by equation (32)

$$\frac{dl}{dt}(u, t) = k(u, t)l^q \quad (32)$$

where q is often set to 0, i.e. linear growth.

Within the Gadget framework it is possible to use other formulations, such as the von Bertalanffy equation, to describe the growth.

In this version of the model, we assume that the growth rate does not vary through the year, i.e. $k(u, t) = k(u, y)$. The year and stock factor $k(u, y)$ can thus be written in a separable way for immature and mature fish:

$$k(u, y) = k_1(y)k_2(u) \quad (33)$$

where $k_2(\text{immature})=1$, $k_2(\text{mature})<1$.

4.4.2 Implementing mean growth in length

After the mean growth for each length group is calculated, the length distributions are updated according to the calculated mean growth. This is done allowing a certain proportions of the fish to grow 0,1,2... length groups (no fish are allowed to shrink). Let

$$\mu_{u,i}(t) = \frac{1}{\Delta L} \frac{dl}{dt}(u, t, l_i) \quad (34)$$

be the mean growth of fishes in population group u and length group i measured in number of length groups and $g_{ij}(u, t)$ be the proportion of fishes in length group i growing to length group j . How $g_{ij}(u, t)$ are selected affects the spread of the length distributions but the following two equations must always be satisfied:

$$\sum_{j=i}^{L_{\max}} g_{ij}(u, t) = 1 \quad (35)$$

and

$$\mu_{u,i}(t) = \sum_{j=i}^{L_{\max}} (j - i) g_{ij}(u, t) \quad (36)$$

(35) ensures that the number of fish is conserved by the growth process, while (36) gives the correct mean growth. The number of fish in each length group after growth has taken place is given by

$$N^{(2)}(u, j, t) = \sum_{i=j-r}^j N^{(1)}(u, i, t) g_{ij}(u, t) \quad (37)$$

As in Björnsson and Sigurdsson (2003), the proportions are selected from a beta-binomial distribution, i.e. a binomial distribution $f(r, g)$ where r is the maximum number of length groups that a fish can grow in one time interval and the probability g comes from a beta distribution, described by parameters α and β (Stefánsson 2001; ICES 2003c). As in all discrete probability distributions equation (35) is automatically satisfied. The mean of this distribution is given by:

$$\mu_{u,i}(t) = \frac{r\alpha_{u,i}}{\alpha_{u,i} + \beta_u} = \sum_{j=i}^{i+r} (j - i) g_{ij}(u, t) \quad (38)$$

If $\mu_{u,i}$ and β_u is given, $\alpha_{u,i}$ can be calculated. β_u , which should be estimated, will affect the spread of the length distribution.

4.4.3 Modelling growth in weight

The variation in weight at length has been large for Northeast Arctic cod. The ratio between the minimum and maximum weight at length (yearly averages) is between 0.65 and 0.80 for pre-spawning females in the 50-90 cm range (Marshall et al. 1998), and variation in the length-weight relationship should thus be modelled. In this paper, we will, however, use the parameters in the maturation function based on this relationship. When this model is extended to multispecies, one may attempt to model growth in weight.

5. Data sources

The data sources available are survey data, commercial catch data and stomach content data. For a description of parameter estimation and objective functions used for fitting such a model to data, see e.g. Frøysa et al. (2002) or Björnsson and Sigurdsson (2003). The model is currently run from 1985 to 2004, with most attention being paid to the period after 1990.

5.1 Survey data

5.1.1 Joint Barents Sea winter survey (bottom trawl and acoustics)

A combined acoustic survey and bottom trawl survey for demersal fish in the Barents Sea has been carried out by Norway in January-March (mostly in February) since 1981. Since 2000, it has been a joint Norwegian-Russian survey. The survey methodology, which has changed somewhat over time, is described by Jakobsen et al. (1997). The time series has been corrected for some of those changes. It should be noted that the survey conducted in 1993 and later years covered a larger area compared to previous years. In 1991 and 1992, the number of young cod (particularly 1- and 2-year old fish) was probably underestimated, as cod of these ages were distributed at the edge of the old survey area. This change in survey coverage is not corrected for. Also note that the change from 35 to 22 mm mesh size in the cod-end in 1994 is not corrected for in the time series. This mainly affects fish < 20 cm. A trawl with 80mm mesh size is used. It is thus likely that the changes mostly affect the estimates of small, young cod. In order to deal with these difficulties data on one and two year old fish prior to 1994 have been excluded from the model.

From this survey, both acoustic and bottom trawl indices of abundance by age and length group are calculated. The survey mainly covers immature fish.

5.1.2 Lofoten acoustic survey on spawners

Since 1985, an acoustic survey has been carried out on the main spawning grounds in the Lofoten area in March/April. A description of the survey, sampling effort and details of the estimation procedure can be found in Korsbrekke (1997). Due to the introduction of new acoustic equipment in 1990, the time series should be split in two parts: 1985-1989 and 1990-present.

5.1.3 Russian autumn survey

The Russian autumn bottom trawl survey (November-December) is described by Lepesevich and Shevelev (1997). This survey covers the entire distribution of the cod stock, and has been carried out since 1982. A trawl with 125 mm mesh size and a 12 mm inner mesh size is used. The catchability of small fish (< 40cm) will thus be much lower than for the Norwegian surveys. This survey provides indices of abundance for all age groups from 0 upwards. (Age 0 indices are at present not available by length). Acoustic indices from this survey are also available, but were excluded from the assessment of cod several years ago because the indices were noisy and the methodology was changed.

Data from this survey in 1994 seem to be an outlier and have been excluded in Fleksibest runs. We exclude them also here. They show up as outliers in the diagnostics of the XSA model (ICES, 2004b).

5.1.4 International 0-group survey

An international 0-group survey has been carried out in the Barents Sea and adjacent waters annually since 1965. These joint Russian-Norwegian investigations (up to 1976 also British) investigations have taken place in late August and early September, with only a few days variation from year to year. The abundance of 0-group fish is found by fishing regularly with

midwater trawl. From 1980, a standard trawling procedure recommended by ICES has been used (Anon. 1983). The data in the annual survey reports (e.g. Anon. 2003b) are reported as a logarithmic abundance index and a length distribution (0.5cm wide length groups).

5.1.5. Age/length/time range of survey data used

Table 1 gives a suggestion for which age, length and time range to use for the surveys in the first version of the model. The population groups that each survey covers are also given.

Survey	Quarter	Year range	Age range	Length range	Length group width	Stock covered
Joint winter bottom trawl - 1	1	1981-1993	3-9	5-90 cm	5 cm	Immature
Joint winter bottom trawl - 2	1	1994-2004	1-9	5-90 cm	5 cm	Immature
Joint winter acoustic - 1	1	1981-1993	3-9	5-90 cm	5 cm	Immature
Joint winter acoustic - 2	1	1994-2004	1-9	5-90 cm	5 cm	Immature
Lofoten acoustic - 1	1	1985-1989	5-12+	55-110 cm	5 cm	Mature
Lofoten acoustic - 2	1	1990-2004	5-12+	55-110 cm	5 cm	Mature
Russian bottom trawl	4	1982-1993 and 1995-2003	1-8	6-106 cm	5 cm	Immature and Mature
International 0-group	3	1965-2003	0	1-15 cm	0.5 cm	0-group

Table 1. Year, age and length range covered by each survey, as well as population groups covered.

The maturity stage and sex is recorded for all fish which are age-determined (1 fish per 5 cm length group in the Joint winter survey, somewhat different routines in the Lofoten and Russian surveys). Thus it is possible to calculate length distributions on 1 cm resolution of immature and mature male and female fish separately for these surveys, while age-length keys should only be calculated by 5 cm length groups.

5.2 Commercial catch data

The catch in numbers at age and length (5 cm length groups) by quarter are available from the following six main fleets, which make up more than 95% of the total catch in all years: Danish seine, handline, longline, gillnet (all these are Norwegian fleets), Norwegian trawl, Russian trawl. In our model runs, we have combined all the fleets except gillnet into one. Thus, we compare observations and model results for the two fleets *combinedfleet* and *gillnet*.

As with the survey data, maturity and sex is determined for all fish, which are aged, and thus the catch may be calculated divided on maturity stage and sex.

5.3 Capelin abundance data

The capelin stock is measured by an acoustic survey in September-October (Gjøsæter et al. 1998; Anon. 2003b). The abundance of capelin at other times of the year should also be calculated. The capelin stock fluctuates strongly from one year to the next (e. g. an increase from 0.8 to 5.8 million tonnes from 1989 to 1990). This rapid fluctuation means that, for example, using the survey estimate from autumn for the entire calendar year is not an appropriate approach.

At present we calculate the capelin abundance in each quarter based on the stock data in ICES (2003b) as follows:

1. quarter: biomass at 1 January biomass - winter fishing
2. quarter: biomass at 1 August x 0.75,
3. quarter: biomass at 1 August
4. quarter: biomass at 1 January in year $y+1$.

6. Overview of model parameters

6.1 Parameters to be estimated by the model

Initial stock abundance: One parameter per age group, giving the number of fish by age group in the initial year. (May fix abundance of ages 7 and older in starting year). The abundance of cohorts spawned in the starting year or later is fit by the annual variation in natural mortality of *Eggsandlarvae*. For each age group, the proportion immature/mature fish and the sex ratio in the first year could either be estimated or taken from survey data.

Length distribution: mean length and standard deviation of mean length (immature and mature fish) for each age group in the starting year. Mean length and standard deviation of mean length of *Eggsandlarvae*/0-group.

Fishing: For each fleet, a time-dependent fishing effort $\xi_f(y)$ (one parameter per year) and a length-dependent selection curve (two parameters).

Cannibalism mortality: Maximum consumption (cannibalism level) κ in equation (22) and the suitability of cod (p_0 in equation 25), and the suitability of capelin and the abundance of other food (equation 27).

Residual natural mortality: One parameter per year for *Eggsandlarvae* and possibly also for 0-group.

Growth: yearly factors $k_1(y)$, one set for 0-group and one for all immature/mature fish, mature growth/immature growth ratio ($k_2(mature)$), one spread parameter (β_u) for 0-group and one for all immature/mature fish.

Maturation: assume no age dependence ($\theta=0$), estimate l_{50} , α , λ , and kn_{50} .

Survey parameters: Parameters in the functions $q_1(p,u,l_i)$ and $q_2(p,u,t)$, 1-3 per survey, depending on whether length-dependence is allowed for or not.

6.2 Parameters fixed externally to the model

The following parameters are fixed externally to the model, using available biological knowledge.

Fishing: Quarterly distribution of fishing effort, based on quarterly distribution of catch in tonnes ($\theta_{q,y}$ in equations (20) and (21)).

Residual natural mortality (for immature and mature fish, AFWG has for many years used $M=0.2\text{year}^{-1}$)

Size dependence of cannibalism (could also be estimated)

Fecundity parameters (equation 13).

7. Parameter estimation

When comparing observations to model results, the Pearson objective function was used (Frøysa et al., 2002).

7.1 Relating survey data to stock abundance

The relationship between the modeled survey index I for survey p , $I(p,u,i,a,t)$, and the population number $N(u,a,i,t)$ can be described by:

$$I(p,u,a,i,t) = \Xi_{p,u}(l_i) q(p,u,t) N(u,a,i,t) \quad (39)$$

where $\Xi_{p,u}(l)$ ($0 \leq \Xi \leq 1$) describes the length selectivity for survey p , analogously to the length selectivity for commercial catch, see equations 15-17. $q(p,u,t)$ describes the time dependence, and i is here set to constant.

Denote the observed survey index by $\hat{I}(p,u,i,a,t)$. The objective function for this survey is then given by

$$L_p = \sum_{i,a,t} \frac{\hat{I}(p,u,i,a,t) - I(p,u,i,a,t)}{I(p,u,i,a,t)^2 + \varepsilon} \quad (40)$$

For the catch data, the comparison was made on a yearly basis. Denote the observed catch by $\hat{C}(f,u,i,a,y)$. The objective function is then given by:

$$L_f = \sum_{i,a,y} \frac{\hat{C}(f,u,i,a,y) - C(f,u,i,a,y)}{C(f,u,i,a,y)^2 + \varepsilon} \quad (41)$$

(Both (40) and (41) need to be adapted to the case where a survey or a fleet catch several population groups)

The total objective function is then given by:

$$L_{tot} = \sum_f w_f L_f + \sum_p w_p L_p \quad (42)$$

, where the weighting factors w_p and w_f were set so that the total contribution to the objective function from survey data and from catch data was approximately equal, and each survey gives an approximately equal contribution.

7.2 Estimation procedure

Parameters are estimated using a two-stage optimisation process, combining Simulated Annealing and a Hooke&Jeeves stepwise estimation procedure. The optimisation begins with Simulated Annealing, which rapidly moves the parameter estimate to a region of possible solutions. Optimisation then switches to the “hill climbing” approach of Hooke&Jeeves, which provides a rapid method of converging to a nearby solution. The optimisation procedure was iterated until successive solutions are identical (ICES 2004c).

8. Model use

A detailed, biologically-based, population model as described here provides a framework for exploring the effect of including detailed process models in a population model. This can be useful both from the point of view of improving the population model, and to test and develop various process sub-models. Because the Fleksibest model has been run for Northeast Arctic Cod at an ICES assessment working group (Arctic Fisheries Working Group), a considerable amount of effort has been put into ensuring that the modelled population has a realistic size and structure.

A biologically detailed cod model as described above may improve the assessment of present and past stock size and allow for better predictions. The inclusion of 0-group and extension of the immature stock down to age 1 should help the assessment by allowing the estimation of the abundance of all age groups in the stock, which can not be done by the present Fleksibest model.

Using an age-and-length based model instead of an age-structured model will in itself result in a revision of the reference points, as the effect of size-dependent mortality on size at age is modelled. Here the work of Kvamme and Frøysa (2004), who studied the influence of length-dependent selectivity curves on stock development using Fleksibest, could be utilised.

9. Results

The closed life cycle model described in this paper produces a stable, biologically realistic, simulation of the Northeast Arctic Cod. The numbers of the spawning stock and the 3+ cod (Figure 2) and the biomass of spawning and 3+ fish (Figure 3) are shown for the duration of the simulation. The equivalent biomass and number predictions from the Arctic Fisheries Working Group XSA assessment (ICES 2004b) are shown for comparison. Both models use essentially the same data sets.

Both models show the same population trends, and have similar sized stocks in both numbers and biomass. Total and spawning stock biomass and numbers are high for most of the 1990s under both models, declining to a low in 1999 and 2000, followed by a rise in the present decade. It can be seen that the two models are in good agreement for biomass (Figure 3), with the exception that the current model suggests that the high stock levels in the mid 1990s resulted in an even higher spawning stock biomass than that predicted by the XSA. The models are also in reasonably good agreement for stock numbers through time (Figure 2).

However the model presented here predicts fewer immature fish after around 1994 than is the case with the XSA. The recent rise in stock numbers is also markedly less pronounced than under the XSA, although the biomasses predicted by the two models is in close agreement in recent years. The total number of fish by age for both models is shown in Figure 4. The discrepancy post 1994 can be seen to be largely due to the current model predicting fewer younger fish, and slightly larger numbers of older fish than the XSA analysis. Thus, although the overall biomasses are similar in the two models, the underlying stock dynamics are slightly different.

The point at which stock numbers diverge in the two models is around 1994, which is the time of an improvement in the Barents Sea Winter Survey (section 5.1.1). After this date the data collected on the smallest fish are considerably improved. It might therefore be reasonable to suppose that the results in the present model, which explicitly considers these smaller fish, are more realistic during this latter part of the simulation period.

The numbers of age 1 and 2 fish are also shown. There is relatively little data available on small (less than 3 years old) fish prior to 1994 (Table 1), making it difficult for the model to assign mortalities from predation to these age groups. Post 1994 the absence of stomach content data in the estimation procedure makes modelling cannibalism length selectivity difficult. Cannibalism of small cod by larger cod is a major source of juvenile mortality. The results for 1 and 2 year old cod should therefore be considered preliminary until the stomach content data has been included.

The model presented here thus produces a realistic simulation of the Northeast Arctic Cod. The model results are broadly similar to those of the XSA model, though with differences in the simulated stock dynamics.

10. Further work

10.1 Including cannibalism data

The cod stomach content data were taken from the joint PINRO-IMR stomach content database. The procedure for sampling and analysis of the stomachs is described by Mehl and Yaragina (1992). The Gadget model calculates consumption, while the observations reflect stomach content at a particular point in time. In order to make a comparison between model results and observations, it is necessary to convert between these two entities (ICES, 2003c). At present, we do this by using the method described by Bogstad and Mehl (1997). This uses the evacuation rate model of dos Santos and Jobling (1995) to convert from stomach content to consumption. It should be noted that the evacuation rate is temperature-dependent.

Data on consumption of cod by cod (cannibalism) are at present available by predator age group and prey length group for each half-year for the period 1984-2003, but it is possible to

prepare the data by predator length groups as well as prey length groups, and on a finer time scale. Including such data in the model would improve the ability to distinguish between mortality on one and two year old fish.

10.2 Including data on first time/repeat spawners

Data from the Lofoten survey split on first-time and repeat spawners could be utilised in the estimation of maturation parameters. The mature stock would then need to be split into two-stocks: First-time spawners and repeat spawners. Splitting the survey in this way gives better possibility for determining the proportion of *maturing* fish, and not only the proportion of *mature* fish.

10.3 Division by sex

Due to differences in growth and maturation, male and female fish could in the future be modelled separately. One would then have to split both immature and mature fish into males and females, and assume a 1:1 sex ratio of 0-group when they move into immature fish.

The difference in maturation between male and female Northeast Arctic cod is described by Ajiad et al. (1999). They found the length at 50% maturity to be about 65 cm for males and 75 cm for females, i.e. a difference of about 10 cm. The growth rate of immature fish is approximately the same for both sexes, but males mature at a smaller size. However, their analysis considered the proportion mature at age/length and not the proportion maturing, which is needed to determine the parameters in equation (4). l_{50} will be sex-dependent, while the other parameters in (4) could initially be assumed to be the same for both sexes.

In a model where fish are divided by sex, equation (12) could be used to model fecundity instead of equation (13).

The proportion of females by length group increases with increasing length (Marshall et al. 1998), and this could be interpreted as indirect evidence of sex differences in growth and/or mortality rates. The sex ratio seems to be close to 1:1 for fish < 90 cm. The results of Beverton et al. (1994) indicate that spawning mortality might be the main component of natural mortality among the mature cod. Jakobsen and Ajiad (1999) found that the data on sex ratio in survey and commercial catch data indicate a higher natural mortality in mature males than in mature females. The difference is close to 0.05 year^{-1} . A first approximation could be to set the spawning mortality M_3 to be 0.05 year^{-1} for males and 0.0 for females, with the sex-independent component of spawning mortality continuing to be modelled as part of M_1 .

It is unclear whether the division into female and male fish will improve the assessment of the present stock size. However, this division should help the study of reference points by allowing for a more realistic fecundity-recruitment relationship.

10.4 Relating growth in length to external factors

Individual growth of Northeast Arctic cod has been shown to be dependent both on capelin abundance (Mehl and Sunnanå 1991), and temperature (Michalsen et al. 1998).

Loeng et al. (1995) found that both mean length during the 0-group survey and growth rate in the period between the early juvenile survey and the 0-group survey are positively correlated with temperature. Several papers studying growth of juvenile (age 0-3) cod have recently been published (Ottersen et al. 2002; Helle et al. 2002; Dalpadado and Bogstad 2004). These papers have related length growth and length-at-age of NEA cod to various biotic and abiotic factors such as cod abundance, cod length at a younger age, food abundance (capelin, zooplankton), temperature and inflow.

Temperature data from several hydrographic sections in the Barents Sea are available. The most frequently used when correlating biological variables to oceanographic conditions is the Kola section (Tereshchenko 1996). A positive relationship has been found between mean individual growth and temperature, see e.g. Jørgensen (1992). The ambient temperature for each age group of cod has also been calculated and related to cod growth (Michalsen et al. 1998). It was found that the mean individual growth was highest for year classes experiencing high temperatures. It is possible to include the effects of temperature on growth within a Gadget model.

The diet of age 1 and younger cod (< 20 cm) mainly consists of invertebrates. The diet changes by cod size, so that cod of age 3 and older (> 30 cm) mainly prey on fish, with capelin as the most important prey species (Bogstad and Mehl 1997). The annual variation in growth rate may thus differ between age 0-2 cod and older cod.

10.5 Other surveys which could be used

The Norwegian bottom trawl survey in the Svalbard and Barents Sea area in August/September is described by Aglen (1999). The Svalbard area has been covered by a bottom trawl survey at this time of the year since 1981, while the Barents Sea has been covered each year since 1995. Since 1995, acoustic abundance indices are available both for the Svalbard area and the Barents Sea. The spatial coverage of the Barents Sea area has, however, been very variable. The methodology used in this survey is essentially the same as in the Joint Barents Sea winter survey.

Indices of abundance of early juvenile cod (age 0) from surveys in June-July are available for the period 1978-1991 (Helle et al., 2000; Helle and Pennington 1999). Mean length and length distributions from this survey are also available. This survey could be used in future studies of the dynamics in the first half-year of life, we do not plan to include it here.

10.6 Multi-species modelling

Cod are a major predator on small fish in the Barents Sea. The ability to model 1 and 2 year-old cod is important in constructing a multi-species model for the Barents Sea. Modelling cod predation on small fish (both cod and non-cod) using the relative proportions of prey species found in cod stomachs requires that all the major prey components be considered. The work presented here on modelling 1 and 2 year-old cod may thus provide an initial step towards extending the cod model to include other species.

11. References

Aglen, A. 1999. Report on demersal fish surveys in the Barents Sea and Svalbard area 1996 and 1997. Fisken og Havet 7-1999, Institute of Marine Research, Bergen, Norway.

Ajiad, A.M., Jakobsen, T., and Nakken, O. 1999. Sexual difference in Maturation of Northeast Arctic Cod. J. Northw. Atl. Fish. Sci. 25:1-15.

Anon. 1983. Preliminary report on the International 0-group fish survey in the Barents Sea and adjacent waters in August-September 1980. Ann. Biol. 37: 259-266.

Anon. 2003a. dst2. Development of Structurally Detailed Statistically Testable Models of Marine Populations. QLK5-CT1999-01609. Progress Report for 1 January to 31 December 2002. Marine Research Institute Report No. 98, Marine Research Institute, Reykjavik, Iceland.

Anon. 2003b. Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea, August-October 2003. IMR/PINRO Joint Report Series 2/2003. ISSN 1502-8828, 51 pp.

Beverton, R. J. H., Hylan, A., and Østvedt, O. J. 1994. Growth, maturation, and longevity of maturation cohorts of Northeast Arctic cod. ICES mar. Sci. Symp. 198:482-501.

Björnsson, H., and Sigurdsson, Th. 2003. Assessment of golden redfish (*Sebastes marinus* L.) in Icelandic waters. Scientia Marina 67(Suppl. 1):301-314.

Bogstad, B. 2002. A model for size preferences in cannibalism in Northeast Arctic cod (*Gadus morhua* L.). Annex C.6 in dst2. Development of Structurally Detailed Statistically Testable Models of Marine Populations. QLK5-CT1999-01609. Progress report for 1 January to 31 December 2001. Marine Research Institute Technical Report no 87, Marine Research Institute, Reykjavik, Iceland, 320 pp.

Bogstad, B. 2003. Modelling of the recruitment process with application to Gadget. Annex D.4 in dst2. Development of Structurally Detailed Statistically Testable Models of Marine Populations. QLK5-CT1999-01609. Progress Report for 1 January to 31 December 2002. Marine Research Institute Report No. 98, Marine Research Institute, Reykjavik, Iceland, 346 pp.

Bogstad, B., Hiis Hauge, K., and Ulltang, Ø. 1997. MULTSPEC – A Multi-Species Model for Fish and Marine Mammals in the Barents Sea. J. Northw. Atl. Fish. Sci. 22: 317-341.

Bogstad, B., Lilly, G. R., Mehl, S., Pálsson, Ó. K., and Stefánsson, G. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland and eastern Newfoundland). ICES mar. Sci. Symp. 198: 576-599.

Bogstad, B. and Mehl, S. 1997. Interactions Between Cod (*Gadus morhua*) and Its Prey Species in the Barents Sea. Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01: 591-615. University of Alaska Fairbanks.

Dalpadado, P., and Bogstad, B. 2004. Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth. Polar Biology 27: 27:140-154.

Dos Santos, J., and Jobling, M. 1995. Test of a food consumption model for the Atlantic cod. ICES J. mar. Sci. 52:209-219.

Frøysa, K. G., Bogstad, B., and Skagen, D. W. 2002. Fleksibest – an age-length structured fish stock assessment tool with application to Northeast Arctic cod (*Gadus morhua* L.). Fisheries Research 55: 87-101.

Gjøsæter, H., Dommasnes, A., and Røttingen, B. 1998. The Barents Sea capelin stock 1972-1997. A synthesis of results from acoustic surveys. Sarsia 83:497-510.

Godø, O. R. 1989. The use of tagging studies to determine the optimal time for estimating acoustic abundance of spawning cod. Fisheries Research 8: 129-140.

Heino, M., Dieckmann, U., and Godø, O.R. 2002. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES Journal of Marine Science 59:562-575.

Helle, K., Bogstad, B., Marshall, C. T., Michalsen, K., Ottersen, G., and Pennington, M. 2000. An evaluation of recruitment indices for Arcto-Norwegian cod (*Gadus morhua* L.). Fisheries Research 48: 55-67.

Helle, K., and Pennington, M. 1999. The relation of the spatial distribution of early juvenile cod (*Gadus morhua* L.) in the Barents Sea to zooplankton density and water flux during the period 1978-1984. ICES Journal of Marine Science 56:15-27.

Helle, K., Pennington, M., Bogstad, B. and Ottersen, G., 2002. Some environmental factors that influence the growth of Arcto-Norwegian cod from the early juvenile to the adult stage. Environmental Biology of Fishes 65:341-348.

ICES 2002. Report of the Study Group on Incorporation of Process Information into Stock-Recruitment Models, Lowestoft, UK 14-18 January 2002. ICES C.M. 2002/C:01, 94 pp.

ICES 2003a. Report of the Study Group on Growth, Maturity and Condition in Stock Projections. Copenhagen, 5-10 December 2002. ICES C.M. 2003/D:01, 95 pp.

ICES 2003b. Report of the Northern Pelagic and Blue Whiting Fisheries Working Group, Copenhagen 29 April – 8 May 2003. ICES C. M. 2003/ACFM:23.

ICES 2003c. Report of the Study Group on Age-Length Structured Assessment Models, Bergen 3-6 June 2003. ICES C.M. 2003/D:07, 88 pp.

ICES 2004a. Report of the Study Group on Growth, Maturity and Condition in Stock Projections. Aberdeen, Scotland, 19-23 January 2004. ICES C.M. 2004/D:02, 66 pp.

ICES 2004b. Report of the Arctic Fisheries Working Group, Copenhagen 4-13 May 2004. ICES C. M. 2004/ACFM:28, 475 pp.

ICES 2004c. An overview of Gadget, the Globally applicable Area-Disaggregated General Ecosystem Toolbox, Vigo 22-25 September. ICES C.M. 2004/FF:13

- Jakobsen, T., and Ajiad, A. M. 1999. Management Implications of Sexual Differences in Maturation and Spawning Mortality of Northeast Arctic Cod. *J. Northw. Atl. Fish. Sci.* 25: 125-131.
- Jakobsen, T., Korsbrekke, K., Mehl, S., and Nakken, O. 1997. Norwegian combined acoustic and bottom trawl surveys for demersal fish in the Barents Sea during winter. *ICES CM* 1997/Y:17.
- Jørgensen, T. 1992. Long-term changes in growth of North-east Arctic cod (*Gadus morhua*) and some environmental influence. *ICES J. mar. Sci.* 49:263-277.
- Korsbrekke, K. 1997. Norwegian acoustic survey of Northeast Arctic cod on the spawning grounds off Lofoten. *ICES C.M* 1997/Y:18.
- Kvamme, C., and Frøysa, K. G. 2004. Assessing the stock effect of selectivity changes in a fishery. *Fisheries Research* (in press).
- Lepesevich, Yu. M., and Shevelev, M. S. 1997. Evolution of the Russian survey for demersal fish: from ideal to reality. *ICES C.M.* 1997/Y:09, 10 pp.
- Loeng, H., Bjørke, H., and Ottersen, G. 1995. Larval fish growth in the Barents Sea. In *Climate change and northern fish populations*. Ed. By R. J. Beamish. *Can. Spec. Publ. Fish. Aqu. Sci.*, 121: 691-698.
- Marshall, C. T., Kjesbu, O.S., Yaragina, N. A., Solemdal, P., and Ulltang, Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Can. J. Fish. Aquat. Sci.* 55:1766-1783.
- Marshall, C. T., O'Brien, L., Tomkiewicz, J., Marteinsdóttir, G., Morgan, M. J., Saborido-Rey, F., Köster, F., Blanchard, J. L., Secor, D. H., Kraus, G., Wright, P., Mukhina, N. V., and Björnsson, H. 2003. Developing alternative indices of reproductive potential for use in fisheries management: case studies for stocks spanning an information gradient. *J. Northw. Atl. Fish. Sci.* 33:161-190.
- Marshall, C. T., Yaragina, N. A., Ådlandsvik, B., and Dolgov, A. V. 2000. Reconstructing the stock-recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential. *Can. J. Fish. Aqu. Sci.* 57:2433-2442.
- Mehl, S., and Sunnanå, K. 1991. Changes in growth of Northeast Arctic cod in relation to food consumption in 1984-1988. *ICES mar. Sci. Symp.* 193:109-112.
- Mehl, S., and Yaragina, N. A. 1992. Methods and results in the joint PINRO-IMR stomach sampling program. In: Bogstad, B. and Tjelmeland, S. (eds.), *Interrelations between fish populations in the Barents Sea. Proceedings of the fifth PINRO-IMR Symposium. Murmansk, 12-16 August 1991. Institute of Marine Research, Bergen, Norway*, 5-16.
- Michalsen, K., Ottersen, G., and Nakken, O. 1998. Growth of North-east Arctic cod (*Gadus morhua* L.) in relation to ambient temperature. *ICES Journal of Marine Science* 55: 863-877.
- Nakken, O. 1994. Trends and fluctuations in the Arcto-Norwegian cod stock. *ICES mar. Sci. Symp.* 198:212-228.

Ottersen, G., Helle, K. and Bogstad, B. 2002. Do abiotic mechanisms determine interannual variability in length-at-age of juvenile Arcto-Norwegian cod? *Can. J. Fish. Aquat. Sci.* 59:57-65.

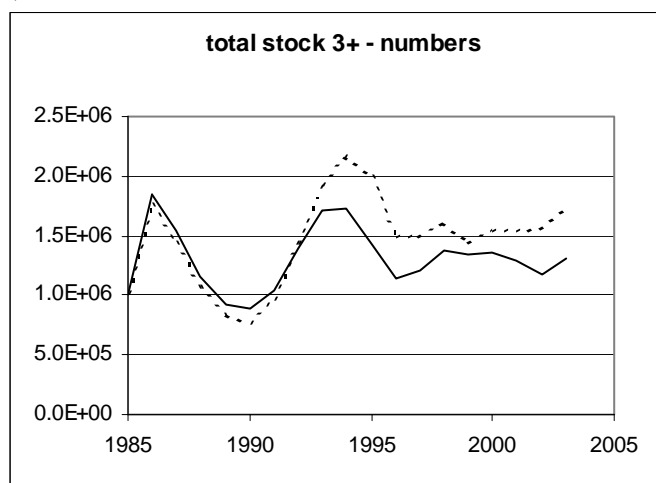
Stefánsson, G. 2001. An implementation of growth. Annex E1 in: Anon. 2001. *dst2. Development of Structurally Detailed Statistically Testable Models of Marine Populations*. QLK5-CT1999-01609. Progress Report for 1 January to 31 December 2000. Marine Research Institute Report No. 78, Marine Research Institute, Reykjavik, Iceland.

Tereshchenko, V. V. 1996. Seasonal and year-to-year variations of temperature and salinity along the Kola meridian transect. *ICES C.M.*1996/C:11, 24 pp.

Ulltang, Ø. 1996. Stock assessment and biological knowledge: can prediction uncertainty be reduced? *ICES Journal of Marine Science* 53: 659-675.

Figures

a)



b)

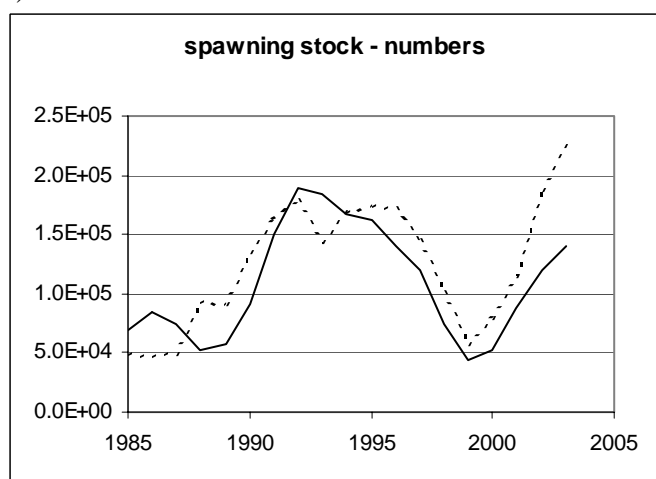
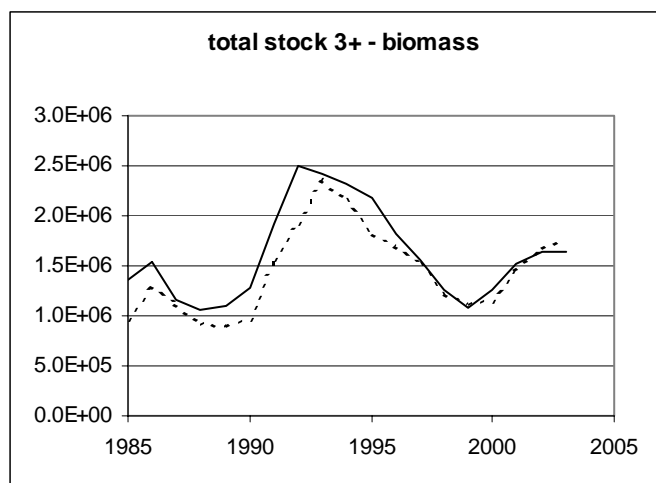


Figure 2. Number of fish of age 3+ (a) and in the spawning stock (b), in million fish. Solid line indicates the closed life cycle model described here, dotted line is the 2004 AFWG XSA assessment.

a)



b)

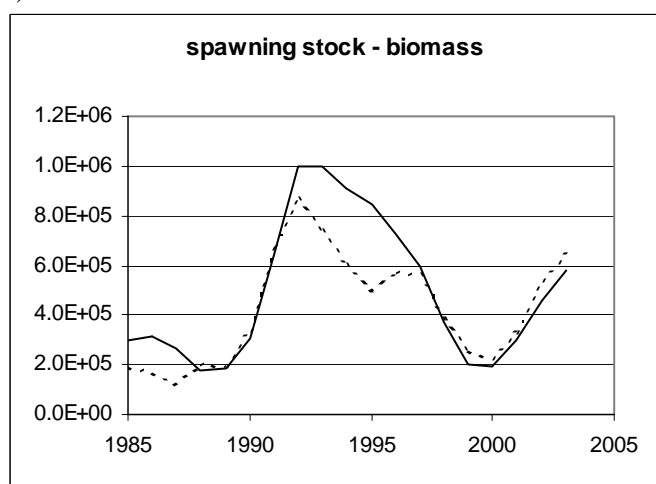


Figure 3. Total biomass fish of age 3+ (a) and in the spawning stock (b), in tonnes. Solid line indicates the closed life cycle model described here, dotted line is the 2004 AFWG XSA assessment.

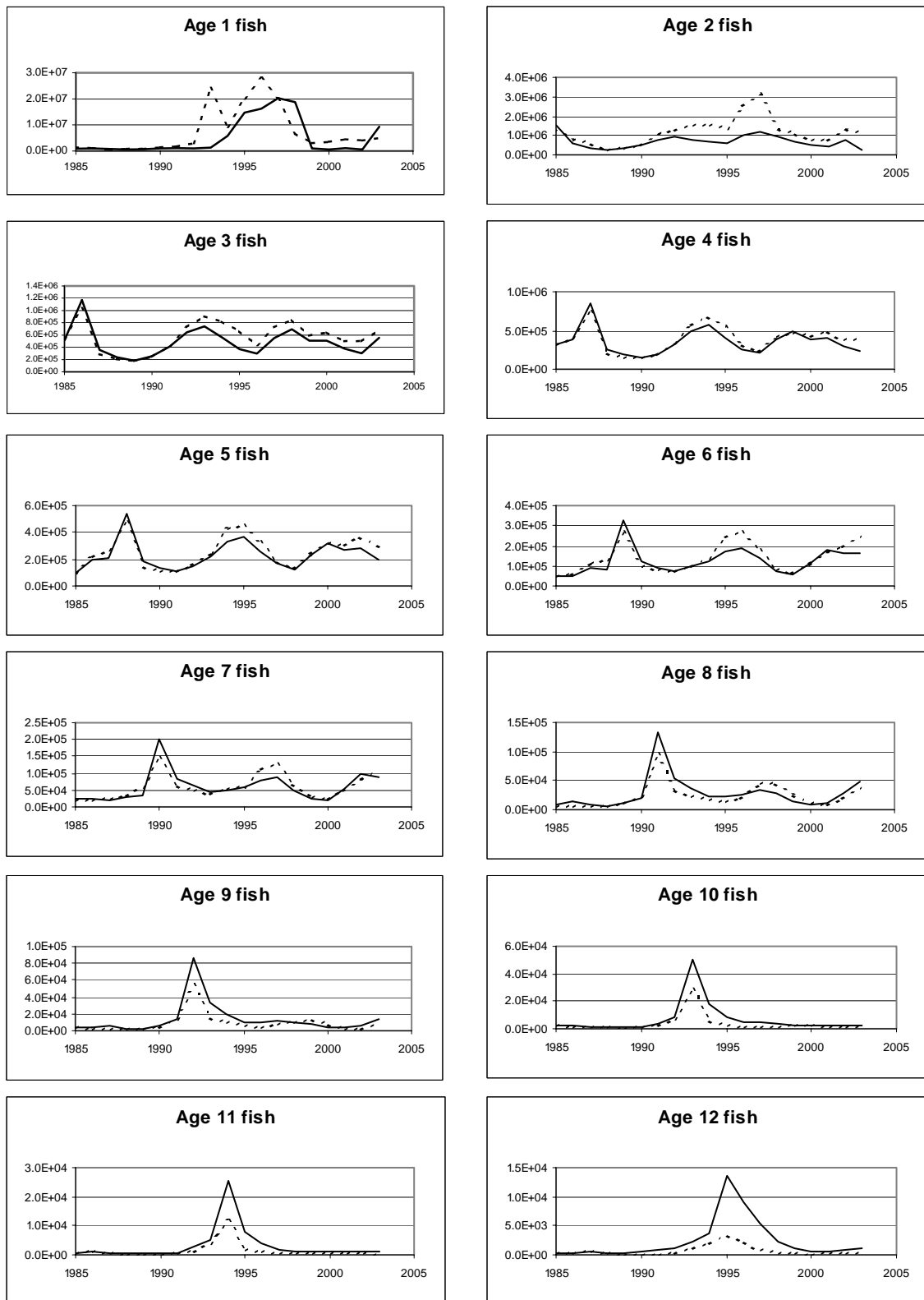


Figure 4. Total number of fish by age, in million fish. Solid line indicates the closed life cycle model described here, dotted line is the 2004 AFWG XSA assessment.